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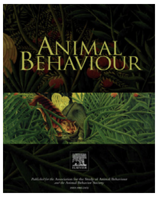

Tropical wrens rely more on acoustic signals than visual signals for inter- and intraspecific discrimination

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Animals may use multiple signalling modalities to discriminate between conspecific versus heterospecific animals, or between individuals that represent a threat versus a mating opportunity. Multimodal signals used in intra- and interspecific discrimination can serve as redundant signals, or each modality may convey unique information. Furthermore, signals in different modalities may show different transmission properties through different habitats. In this study we investigated how two congeneric wrens, rufous-and-white wrens, *Thryophilus rufalbus*, and banded wrens, *Thryophilus pleurostictus*, use acoustic and visual signals for species discrimination in tropical forest habitats. We coupled song playback experiments with visual models to assess the importance of these signals, both in combination and in isolation. We assessed vegetation density in the territories of both species to assess whether more densely vegetated territories influence the use of visual signals. We presented both rufous-and-white wrens and banded wrens with conspecific and congeneric song treatments, model treatments and song-accompanied-by-model treatments. We found that both species responded strongly to song and song-accompanied-by-model treatments, but showed little or no response when the model was presented alone. These results suggest that wrens rely heavily on acoustic signals and very little on visual signals for discrimination. The species differed in their response to conspecific and congeneric trials, with rufous-and-white wrens showing little response to the congeneric trials but banded wrens responding strongly to both conspecific and congeneric trials. The asymmetrical response to the playback trials suggests that there may be a social dominance relationship between these two species, with rufous-and-white wrens being dominant over banded wrens. No previous studies have investigated the relative importance of acoustic and visual signals in males and females for species discrimination. Our results suggest that acoustic signals are more important than visual signals for inconspicuous animals living in dense environments.

Closely related species that live in sympatry and compete for resources should distinguish between individuals that are a competitor species and individuals that represent viable mates (Bradbury & Vehrencamp, 2011). Animals may use a diversity of signal modalities for intra- and interspecific discrimination, such as visual, acoustic, electrical and chemical signals, and many animals appear to use multiple signals simultaneously (Bradbury & Vehrencamp, 2011; Grether, 2011). Several hypotheses have been proposed to explain the benefits of multimodal signals, with two hypotheses receiving considerable attention. The first hypothesis proposes that multimodal signals serve as redundant signals and act as a backup for more accurate information transmission (Anderson, DuBois, Piech, Searcy, & Nowicki, 2013; Partan & Marler, 2005). The second hypothesis proposes that each signal conveys unique information (Hebets & Papaj, 2005). Under either scenario, multimodal signals allow for more efficient and accurate intra- and interspecific discrimination.

The environment modifies the transmission of signals, and we therefore expect habitat to have a strong influence on how animals use multimodal signals (Grether, 2011; Higham & Hebets, 2013; Morton, 1975; Wilkins, Seddon, & Safran, 2012). Acoustic signals are often used for long-range recognition because they can travel around obstructions, but they may not be easily accessible in noisy environments and they may be prone to eavesdropping by unintended receivers (Bradbury & Vehrencamp, 2011; Mennill, Boag, & Ratcliffe, 2002; Wilkins et al., 2012). Visual signals can be easily obstructed by vegetation and therefore work best in open habitats

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or for close-range recognition (Uy & Safran, 2013). Depending on the habitat and the social context, animals may rely heavily or exclusively on a single modality with optimal transmission features. A variable environment may promote the use of multimodal signals so that different signals can convey information in spite of variable barriers to transmission. Bornean rock frogs, *Staurois parvus*, for example, are thought to have evolved multimodal signals to overcome noise in their streamside habitat; males modify the pitch, amplitude and duration of advertisement calls to maximize signal transmission and they also use numerous visual signals to communicate in a noisy environment (Grafe et al., 2012).

In dense habitats, acoustic signals are mainly used for long-range recognition whereas visual signals are mainly used for close-range recognition (Uy & Safran, 2013) and animals may benefit by using both signal modalities for efficient intra- and interspecific discrimination. In one study, male poison-dart frogs, *Epipedobates femoralis*, responded more strongly to a conspecific male model when its vocal sac was inflated and pulsating and accompanied by a male call, indicating that they used both visual and acoustic signals for species discrimination (Narins, Hödl, & Grabul, 2003). Only three studies have investigated the simultaneous use of visual and acoustic signals for species discrimination in birds. In a study conducted on European warblers, playback accompanied by taxidermic models revealed that male blackcaps, *Sylvia atricapilla*, defending resources against garden warblers, *Sylvia borin*, used both acoustic and visual signals for species discrimination (Matyjasiak, 2004). A study of chestnut-bellied flycatchers, *Monarcha castaneiventris*, found that birds used both song and plumage signals for species discrimination (Uy, Moyle, & Filardi, 2009), but an additional study of this species revealed that these signals were assessed sequentially in dense habitats, with song being used for long-range recognition followed by plumage at close range, whereas song and plumage were used simultaneously in open habitats (Uy & Safran, 2013).

Multimodal signals may help animals discriminate between conspecific and heterospecific individuals, ensuring that aggression is properly directed towards the more threatening conspecific individuals that might usurp their mate and resources (Benites, Campagna, & Tubaro, 2014; Jankowski, Robinson, & Levey, 2010; Ord & Stamps, 2009). However, when conspecific and heterospecific animals use similar resources, it is beneficial to direct aggression towards conspecific as well as heterospecific rivals (Greenberg, Ortiz, & Caballero, 1994; Kodric-Brown & Brown, 1978; Ord & Stamps, 2009). This is especially true with closely related species that compete for common resources and interact aggressively (Catchpole, 1978; Peiman & Robinson, 2010). Heterospecific aggression is widespread in animals (Peiman & Robinson, 2010), but is often asymmetrical, with one species being dominant over the other (Martin & Dobbs, 2015; Martin & Martin, 2001; Pearson & Rohwer, 2000). Asymmetrical competition may be involved in niche partitioning in closely related sympatric species (Dingle, Poelstra, Halfwerk, Brinkhuizen, & Slabbekoorn, 2010) and can influence which species use particular resources (Carrete et al., 2010; Farwell & Marzluff, 2013; Peiman & Robinson, 2010). Commonly, the subordinate species is forced to inhabit less desirable territories (Jankowski et al., 2010; Morse, 1974; Pearson & Rohwer, 2000). For example, Townsend's warblers, *Dendroica townsendi*, exhibit more aggression than hermit warblers, *Dendroica occidentalis*; Townsend's warblers outcompeted and replaced hermit warblers, thereby shifting their hybrid zone (Pearson & Rohwer, 2000). In some cases, the subordinate species will reduce singing and avoid the dominant species. For example, subordinate mountain wrens, *Troglodytes solstitialis*, sang fewer songs and stayed farther from the speaker when presented with the songs of dominant house wrens, *Troglodytes aedon* (Martin & Dobbs, 2015). However, this asymmetric relationship is not universal. For example, subordinate mountain chickadees, *Poecile gambeli*, responded aggressively to both conspecific and heterospecific songs of the dominant black-capped chickadees, *Poecile atricapillus* (Grava, Grava, & Otter, 2012).

In this study, we combined song playback with presentation of visual models to investigate the importance of acoustic and visual signals for intra- and interspecific discrimination in two closely related species: rufous-and-white wrens, *Thryophilus rufalbus*, and banded wrens, *Thryophilus pleurostictus*. These two species nest primarily in bullhorn acacia trees, *Vachellia collinsii* (Joyce, 1993; Molles & Vehrencamp, 1999) and occupy similar foraging niches (Ahumada, 2001; Molles & Vehrencamp, 1999). Rufous-and-white and banded wren territories do not overlap (at our study site rufous-and-white wrens occupy mature, evergreen forest and banded wrens inhabit drier, second-growth forest), but they often hold neighbouring territories, and we have observed aggressive competitive interactions between them in the field (Hick, Doucet, & Mennill, 2015). Our objective was to assess the importance of acoustic and visual signals for intra- and interspecific discrimination in these sympatric Neotropical wrens. We delivered both conspecific and congeneric song playback, visual model presentation, and a combination of both song and model presentation to both males and females of the two species. Given our anecdotal observation that the mature evergreen forests preferred by rufous-and-white wrens appear to be more densely vegetated, we quantified vegetation density in the two species' territories. Given our anecdotal observation that there are fewer acacia nesting trees in the evergreen forest habitat of rufous-and-white wrens, we collected acacia tree abundance data to better understand the distribution of one potentially limiting resource for these two species. We were also interested in assessing the possibility that interspecific dominance mediates interactions between rufous-and-white wrens and banded wrens, especially in light of the results of a previous playback study showing that rufous-and-white wrens display little aggression towards banded wren song playback (Hick et al., 2015). We tested four main predictions in this study: (1) rufous-and-white wrens and banded wrens would use multimodal signals for species discrimination, but would rely more heavily on acoustic signals than visual signals because of their cryptic plumage and densely foliated habitats; (2) banded wrens would have less densely vegetated territories, and therefore would rely more heavily on visual signals than rufous-and-white wrens, even though both species would still rely heavily on acoustic versus visual signals; (3) the smaller-bodied banded wrens would show high aggression towards both the conspecific and heterospecific stimuli, whereas the larger-bodied rufous-and-white wrens would show more aggression towards conspecific stimuli than heterospecific stimuli; (4) males and females would show similar responses to all treatment types, but overall, males would respond more than females.

METHODS

General Field Methods

We conducted this research in Sector Santa Rosa (10°40′N, 85°30′W), of the Guanacaste Conservation Area in northwestern Costa Rica, a lowland dry-forest site. We conducted playback experiments from early April to early June 2014, during the end of the dry season and the beginning of the rainy season. At this time of year, wrens build nests and defend territories (Topp & Mennill, 2008) and both study species are responsive to playback (e.g. Mennill, 2006; Molles & Vehrencamp, 2001). We conducted all playback and model presentation experiments between 0630 and 1100 hours, a time of day when countersinging interactions are common for both species (Mennill & Vehrencamp, 2005; Molles & Vehrencamp, 1999).

As part of our long-term study of this population of rufous-and-white wrens, we uniquely colour-banded as many animals as possible to facilitate identification in the field ($N = 32$ of 38 rufous-and-white wrens were uniquely colour-banded). We banded only 2 of 34 banded wrens. For unbanded birds of both species, we distinguished between pairs based on their ongoing occupation of the same area, an approach that has proven effective in previous studies of both species (e.g. Battiston, Wilson, Graham, Kovach, & Mennill, 2015; Hick et al., 2015; Kovach, Hall, Vehrencamp, & Mennill, 2014; Mennill, 2006; Vehrencamp, Ellis, Cropp, & Koltz, 2014). We discriminated between males and females based on their sex-specific vocal traits (Hall, Rittenbach, & Vehrencamp, 2015; Mennill & Vehrencamp, 2005; Molles & Vehrencamp, 1999).

Playback Treatments

To study the role of acoustic and visual signals in species discrimination, we conducted experiments involving both rufous-and-white wrens and banded wrens. We used playback accompanied by a wooden model to simulate the presence of birds in wren territories. For each species, we delivered a song playback treatment (hereafter 'song treatment'), a model-only treatment (hereafter 'model treatment'), and a treatment that featured both a model and song playback (hereafter 'model + song treatment'). In total, each pair received six treatments: (1) a conspecific song treatment, (2) a conspecific model treatment, (3) a conspecific model + song treatment, (4) a congeneric song treatment, (5) a congeneric model treatment and (6) a congeneric model + song treatment.

Model Preparation

We chose to use wooden models to simulate both rufous-and-white and banded wrens; taxidermic mounts were not available for use as visual stimuli, and we did not wish to sacrifice live animals to create mounts. The wooden models were carved by skilled wood carvers from the Windsor Wood Carving Museum in Windsor, Ontario, Canada. We produced 10 carved models of the two species (5 of each species) that were the same size (130 mm from end of bill to end of tail; the mean size between the two wren species). When painting the wooden models, we selected paint colours that matched reflectance spectra of museum specimens (see Figs. 1 and 2a, b). We measured spectral reflectance of both the models and museum specimens using an Ocean Optics USB 2000 spectrometer and a PX-2 Flash lamp (Ocean Optics, Dunedin, FL, U.S.A.). The reflectance probe was mounted in a black rubber holder to exclude all external light and keep the probe perpendicular to the feather surface at a fixed distance of 5 mm. Working at the University of Michigan Museum of Zoology in Ann Arbor, Michigan, U.S.A., we measured plumage reflectance of 11 rufous-and-white wren and 13 banded wren study skins collected from the Guanacaste Region in Costa Rica (previous research has shown that reflectance spectra from museum specimens can accurately represent the coloration of live birds; Doucet & Hill, 2009). We collected five reflectance measurements for each of 10 body regions: belly, breast, crown, flank, mantle, black retrix, brown retrix, rump, undertail coverts and wing primaries. We measured reflectance spectra as the total reflectance across 300 nm–700 nm, the bird-visible spectrum. Both species are sexually monochromatic (Brewer, 2001), and our measurement of 10 females and 14 males revealed no noticeable differences between the sexes' reflectance curves. Neither species exhibited substantial reflectance in the ultraviolet range. We then tried to match the feather and paint colour reflectance curves as closely as possible. We placed mixed paint samples on plain white paper and collected five reflectance measurements for the breast, black rectrices and mantle colours. We continued this process until the reflectance curves were as similar as possible to the curves measured from the specimens. We used the same colours for both species as the reflectance curves for the breast, black rectrices and mantle colours did not differ among museum specimens of rufous-and-white wrens and banded wrens.

Figure 1. Photograph of a rufous-and-white wren (left) looking at a wooden model of a rufous-and-white wren (right).

Playback Stimuli

We generated playback stimuli by extracting songs from recordings collected at our study site over the previous 13 years. Given that the wooden models simulated strangers rather than neighbours, we chose to use playback to simulate the vocalizations of strangers rather than neighbours. To ensure that the stimuli were unfamiliar to the subjects, we used recordings that were collected ≥2 km away from the subjects' territories. Playback stimuli were composed of male solo songs repeated at a rate of one song every 10 s for a total of 5 min. This song rate falls in the natural range of singing behaviour for males of both study species (Mennill & Vehrencamp, 2005; Molles & Vehrencamp, 1999). We chose to focus on male solo songs in this experiment because although rufous-and-white wrens are well known for their vocal duets, female song is uncommon in banded wrens (Hall et al., 2015; Molles & Vehrencamp, 1999; in response to our trials, 3% of banded wren songs were duets, whereas 11% of rufous-and-white wren songs were duets). Furthermore, in both rufous-and-white wrens and banded wrens, males have higher song output than females (Mennill & Vehrencamp, 2005; Molles & Vehrencamp, 1999; Topp & Mennill, 2008) and males respond more intensely to playback than females (Hall, Illes, & Vehrencamp, 2006; Hall et al., 2015; Mennill, 2006; Mennill & Vehrencamp, 2008).

We generated a playback lure to attract the birds to the playback area to ensure that all birds began the trials in a similar location and to ensure that they would be within sight of the model. The lure stimuli included both songs and calls. The lure began with a species-specific song repeated five times at a rate of one song every 10 s, followed by 10 s of species-specific calls (including whoops, rattles and ticking) followed by 5 s of silence repeated for a total of 5 min. The same lure stimulus was used in all treatments for each species to ensure that the aggressiveness of the calls presented did not influence the subjects' response.

We prepared all stimuli using Audition software (v.3.0; Adobe, San Jose, CA, U.S.A.). We selected one song or set of calls from each source recording, choosing a song or call with a high signal-to-noise ratio (assessed visually based on the spectrograms). We filtered out background noise with an 800 Hz high-pass filter (800 Hz is less than the minimum frequency of all songs and calls in this data set).

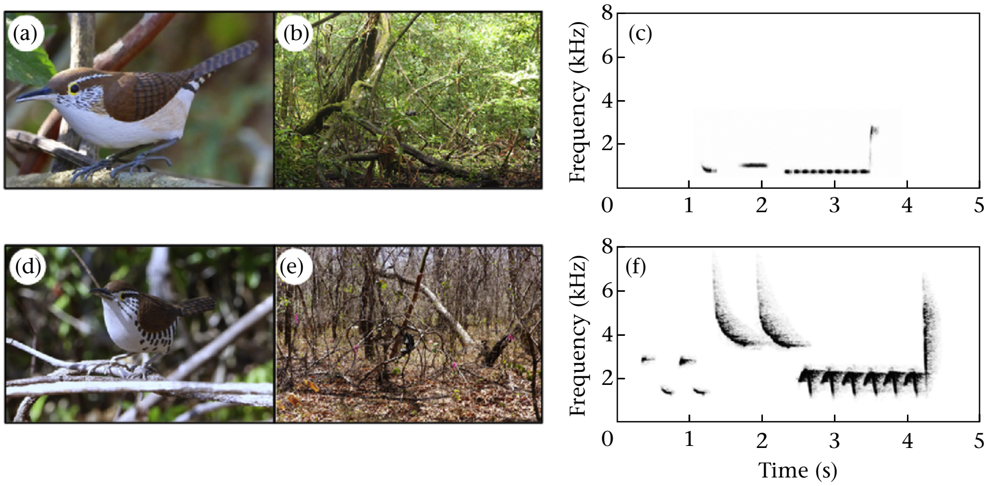

Figure 2. Photographs of (a) a wooden model of a rufous-and-white wren and (b) the habitat in a rufous-and-white wren breeding territory, and (c) a spectrogram of a rufous-and-white wren song. Photographs of (d) a wooden model of a banded wren and (e) the habitat in a banded wren breeding territory, and (f) a spectrogram of a banded wren song. Both habitats were photographed at the same time of year, at the end of the dry season, when birds were nest building.

We standardized amplitude to −1 dB so that all stimuli would be broadcast at the same amplitude.

Playback Technique

We presented each song stimulus a maximum of two times (never twice to the same birds) and we used 10 different models (5 of each species), in alternation, to minimize pseudoreplication. The playback speaker and model were set up within 10 m of a nesting tree near the centre of a pair's territory to simulate competition over their shared resource. The lure speaker was set up 10 m away from the main playback speaker. Once the focal pair was silent for at least 1 min, the trial began with the lure phase followed by the playback phase. The lure phase continued either until a focal bird was within 5 m of the lure speaker, or for a maximum of 5 min (average ± SE length of lure presentation: rufous-and-white wrens: 161.0 ± 9.5 s; banded wrens = 204.2 ± 13.4 s). If the birds did not respond to the first lure, we initiated a 2 min silent period followed by another 5 min lure period. If the focal bird still did not come within 5 m of the lure speaker after two lure phases, we terminated the trial ($N = 7$ trials were terminated for this reason). During the lure phase, the model was covered with camouflage mesh fabric that the observer could slowly pull aside using fishing line. Once the bird was within the experimental area, the 5 min trial began from the playback speaker with either acoustic stimuli, the presence of a model, or both acoustic stimuli and model presentation, followed by a 5 min silent observation period. To minimize carryover effects, each treatment was presented on separate, consecutive days, at the same time of day for each subject. To minimize order effects, we used a factorial design to determine the order of the treatments.

The playback apparatus was a camouflaged, wireless speaker (Scorpion TX200, FOXPRO Inc., www.foxpro.com) hung in vegetation 1 m above the ground, with the model perched on a branch within 0.5 m above the speaker. All treatments were played back at 85 dB SPL as measured with a sound level meter (Casella CEL-240 digital sound level meter; C-weighting, fast response) positioned 1 m in front of the speaker. Banded wrens appear to produce louder songs than rufous-and-white wrens, and this amplitude reflects the average amplitude between the values that have been used in previous playback studies with the two species (80 dB SPL has been used in playback studies of rufous-and-white wrens, and 90 dB SPL in studies of banded wrens; Kovach et al., 2014; Mennill, 2006; Molles & Vehrencamp, 2001), thereby ensuring that amplitude was not a confounding factor.

An observer (K.G.H.) sat concealed in vegetation 15–20 m from the speaker and recorded all treatments using a shotgun microphone (Sennheiser MKH70) and a digital recorder (Marantz PMD660). Flagging tape was placed 2 m on either side of the playback speaker or model to aid in estimating the distance between the responding birds and the simulated intruder (i.e. the loudspeaker and/or model). Throughout the trial period the observer quietly dictated the birds' identities as well as their behaviour and location in relation to the speaker. Trials where neighbouring pairs responded to the playback were aborted and repeated at least 1 week later. We conducted playback experiments on 22 rufous-and-white wren territories and 21 banded wren territories. Of the 22 rufous-and-white wren pairs, one pair had one unsuccessful treatment out of six because they did not respond to the lure for one treatment (conspecific model). Of the 21 banded wren pairs, four pairs had one unsuccessful treatment (1 conspecific song, 2 conspecific model, and 1 conspecific model + song) and one pair had two unsuccessful treatments (conspecific model and congeneric song). This lack of response to the lure could be due to habituation, as four out of the seven unsuccessful treatments were given as the fifth or sixth treatments. However, we were unable to repeat these trials because of time constraints.

Response Measures

We visualized the audio recordings of the playback trials using Syrinx-PC sound analysis software (J. Burt, Seattle, WA, U.S.A.). We annotated all songs and duets as well as the behaviour of the focal pair as dictated by the observer, creating a time-stamped record of all behavioural and acoustic measures. For each male and female subject, we extracted the following response variables: (1) distance of closest approach to the playback apparatus, (2) latency to approach within 5 m of the playback apparatus, (3) number of songs initiated (the number of solo songs plus the first song in a duet) and (4) number of duets created (the number of songs where the subject sang in response to its partner, thus creating a duet). However, we did not analyse the number of duets created when looking at banded wren responses since males and females do not routinely perform vocal duets (Hall et al., 2015; Molles & Vehrencamp, 1999).

Vegetation Measurements

We were interested in quantifying both visual obstruction due to vegetation density as well as nesting tree resource abundance to understand whether this might affect transmission of visual and acoustic signals for species discrimination. We collected vegetation data in late May and early June, 2014. We collected data in 21 rufous-and-white wren and 22 banded wren territories. We followed previously used methods (see Roovers, Bossuyt, Gulinck, & Hermy, 2005; Vermeire & Gillen, 2001) to calculate visual obstruction by using a 1 m high pole divided into alternating red and white 10 cm sections. The pole was placed perpendicular to the ground at the playback location where an observer counted the number of 10 cm sections that were visible at distances of 5 m, 10 m and 15 m. All three distances were measured in all four cardinal directions relative to the playback location.

To better assess the competition between rufous-and-white wrens and banded wrens over a shared resource, we investigated the abundance of one of the primary resources for which they appear to compete: acacia nesting trees. We counted the number of acacia trees in 22 rufous-and-white wren and 21 banded wren territories. We then calculated the number of acacia trees per hectare of territory for each species to assess the resource's availability (average territory size measurements taken from Mennill & Vehrencamp, 2008 for rufous-and-white wrens, and Trillo & Vehrencamp, 2005 for banded wrens).

Statistical Analysis

We analysed our data using generalized linear mixed models (GLMMs). This method allowed us to use a random effect while accounting for non-normal data (several of our response measures could not be normalized due to a preponderance of high and low values); this method also allowed us to include six subjects that responded to some, but not all, of the treatments (Bolker et al., 2008). We included pair identity as a random factor since most pairs received all six treatments. When investigating variation in response between the two focal species, our model included five main factors: (1) subject species (two levels: rufous-and-white wren or banded wren); (2) treatment type (three levels: model, song or model + song); (3) stimulus species (two levels: conspecific or congeneric); (4) sex (two levels: male or female); and (5) playback order (six levels: first – sixth). We used a Poisson error distribution with a log link function for the acoustic variables (songs initiated and duets created) and a Gamma distribution with a log link function for the behavioural variables (distance of closest approach and latency to 5 m). GLMMs with a Poisson error distribution have previously been used for social interaction variables with skewed count data, and Gamma distributions have been used for noncount data skewed to higher values (e.g. Hasegawa, Ligon, Giraudeau, Watanabe, & McGraw, 2014; Santos, Maia, & Macedo, 2009). We ran post hoc pairwise comparisons for all interactions included in our planned comparisons (see below). To adjust for multiple comparisons, we used a sequential Bonferroni correction, which increases P values (instead of decreasing the alpha value); we report corrected P values. When analysing visual obstruction and vegetation data we used Mann–Whitney U tests to compare non-normal data between the two species habitats. We conducted all analyses using SPSS software (v.21; IBM, Armonk, NY, U.S.A.).

We conducted planned comparisons to test our four predictions using the aforementioned statistical analyses. (1) To test our first prediction (that both species would respond more strongly to acoustic signals than visual signals), we focused on the main effect of treatment. If our prediction held true, we expected a significant effect of treatment and that post hoc comparisons would show higher responses to treatments containing acoustic stimuli. (2) To test our second prediction (that banded wrens would rely more heavily on visual signals than rufous-and-white wrens), we focused on the treatment × subject species interaction. If our prediction held true, we expected this interaction to be significant and post hoc analysis to show stronger responses from banded wrens when the treatment included a visual stimulus. (3) To test our third prediction (that smaller-bodied banded wrens would show equivalent responses to both conspecific and congeneric treatments, but larger-bodied rufous-and-white wrens would show a stronger response to conspecific stimuli), we focused on the subject species × stimulus species interaction. If our prediction held true, we expected post hoc analysis to show equivalent responses for the banded wrens in this interaction term, but different responses for the rufous-and-white wrens. (4) To test our fourth prediction (that males would respond more strongly than females, although they would respond similarly to the different treatment types), we focused on the main effect of sex, as well as the interaction between sex × treatment type × stimulus species.

RESULTS

Use of Acoustic versus Visual Signals

To test our first prediction, that both species would respond more strongly to acoustic versus signals, we tested for a main effect of treatment. All of our response measures showed a significant effect of treatment (Table 1, Supplementary Tables S1–S4). For distance of closest approach and latency to approach within 5 m of the playback apparatus, rufous-and-white wrens and banded wrens responded strongly to the song treatment and the model + song treatment and showed weak responses to the model treatment (Fig. 3a, b, Supplementary Tables S1 and S2). We found the same trend for the number of songs initiated (Fig. 3c, Supplementary Table S3). Wrens created significantly more duets in response to the song treatment versus the model treatment, but there was no difference in their response to the model + song treatment and the song or model alone treatments (Fig. 3d, Supplementary Table S4). These results support our first prediction, showing that birds responded more strongly to the treatments that included an acoustic signal.

To test our first prediction separately for each species, we focused on the interaction effect of treatment type × subject species. The results for the distance of closest approach to the loudspeaker as well as latency to approach within 5 m of the loudspeaker supported our first prediction: rufous-and-white wrens approached more closely for the model + song treatment and the song treatment versus the model treatment (Fig. 4a, Supplementary Tables S1 and S2), but showed no difference in their latency to approach during the model + song treatment and the song treatment (Fig. 4b, Supplementary Tables S1 and S2). However, contrary to our first prediction, the number of songs initiated and the number of duets created by rufous-and-white wrens did not differ between three treatment types (Fig. 4c, Supplementary Tables S3 and S4). There was one instance where a rufous-and-white wren male attacked a model, which occurred three times during the same congeneric model + song treatment.

The distance of closest approach and the latency to approach within 5 m of the playback apparatus for banded wrens also supported our first prediction and showed a significant effect of treatment type (Supplementary Tables S1 and S2), with banded wrens approaching the song treatment and the model + song treatment more closely than the model treatment (Fig. 4a, b, Supplementary Tables S1 and S2). There was no significant difference between the distance of closest approach to the song

Table 1
Generalized linear mixed model results of the response of rufous-and-white wrens to playback and model presentation simulating conspecific and congeneric intruders

	Distance of closest approach			Latency to approach within 5 m			Number of songs initiated			Number of duets created		
	F	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*
Treatment type	**25.5**	**2, 461**	**<0.0001**	**23.91**	**2, 461**	**<0.0001**	**9.86**	**2, 461**	**<0.0001**	**5.23**	**2, 461**	**0.006**
Subject species	**6.8**	**1, 461**	**0.009**	2.95	1, 461	0.09	2.27	1, 461	0.13	**15.51**	**1, 461**	**<0.0001**
Stimulus species	**9.01**	**1, 461**	**0.003**	1.03	1, 461	0.31	**16.89**	**1, 461**	**<0.0001**	0.31	1, 461	0.58
Sex	**459.19**	**1, 461**	**<0.0001**	**142.59**	**1, 461**	**<0.0001**	**2266.16**	**1, 461**	**<0.0001**	**18.98**	**1, 461**	**<0.0001**
Playback order	**2.69**	**5, 461**	**0.02**	**2.46**	**5, 461**	**0.03**	**15.56**	**5, 461**	**<0.0001**	**26.66**	**5, 461**	**<0.0001**
Treatment type∗subject species	0.45	2, 461	0.64	0.4	2, 461	0.67	**19.78**	**2, 461**	**<0.0001**	2.68	2, 461	0.07
Subject species∗stimulus species	2.36	1, 461	0.13	0.22	1, 461	0.64	**19.11**	**1, 461**	**<0.0001**	0.21	1, 461	0.64
Sex∗treatment type∗stimulus species	**3.55**	**5, 461**	**0.004**	**3.58**	**5, 461**	**0.003**	**4.9**	**5, 461**	**<0.0001**	**2.56**	**5, 461**	**0.027**

Significant values shown in bold.

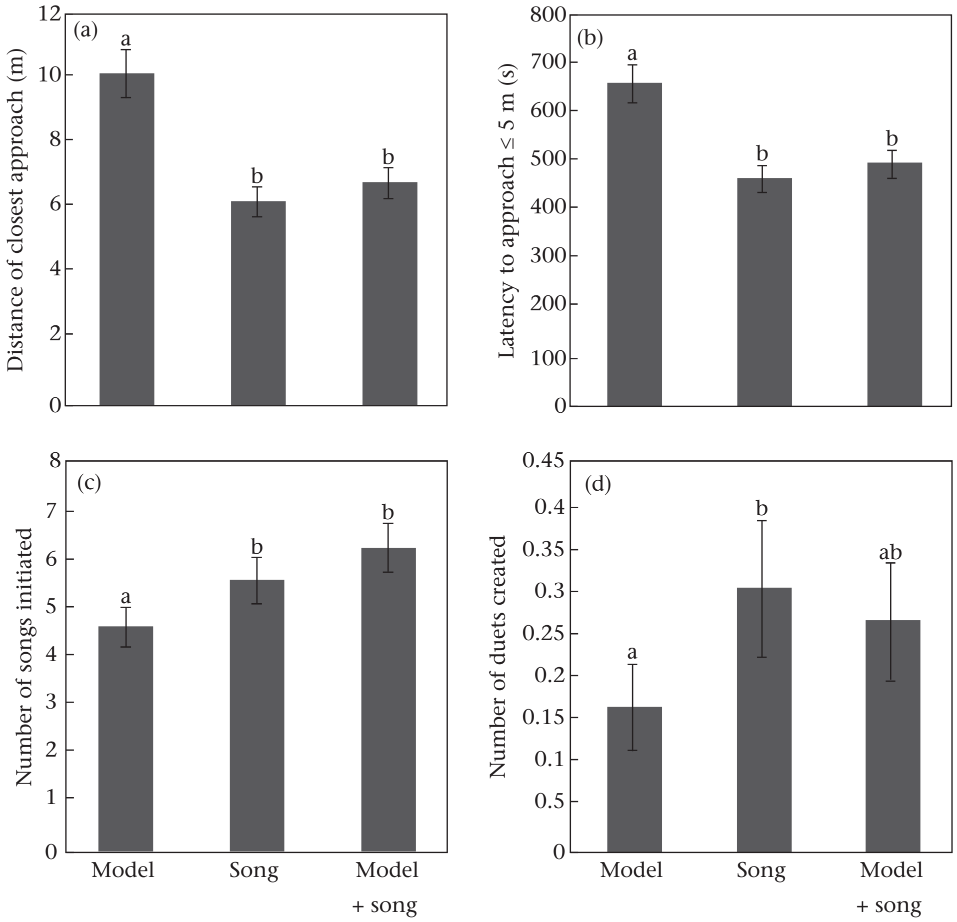

Figure 3. Combined responses of rufous-and-white wrens and banded wrens to model presentation (model), song playback (song) and model presentation + song playback (model + song). (a) Distance of closest approach to the playback speaker and/or model. (b) Latency to approach within 5 m of the playback apparatus. (c) Number of songs initiated (number of solos plus first song of a duet). (d) Number of duets created (song sung in response to a solo song). Different letters above bars indicate statistical significance. Graph shows mean + SE values from treatment type post hoc pairwise comparisons.

treatment and the model + song treatment (Fig. 4a, Supplementary Tables S1 and S2). Banded wrens sang more songs in response to the model + song treatment than in response to the other two treatments (Fig. 4c, Supplementary Table S3), and they sang the fewest songs in response to the model treatment, with an intermediate response to the song treatment (Fig. 4c, Supplementary Table S3). Overall, banded wrens sang significantly fewer duets than rufous-and-white wrens, but they did not differ significantly in their responses to three treatment types (Supplementary Table S4).

Effect of Vegetation Density on Use of Signals

To test our second prediction, that banded wrens would have less densely vegetated territories than rufous-and-white wrens and thus rely more on the visual signal than rufous-and-white wrens, we measured vegetation characteristics in order to better understand visual obstruction within the territories of our two study species, as well as the relative degree of limitation of their nesting substrate: bullhorn acacia trees. Contrary to our second prediction, we found no significant difference in the percentage of visual

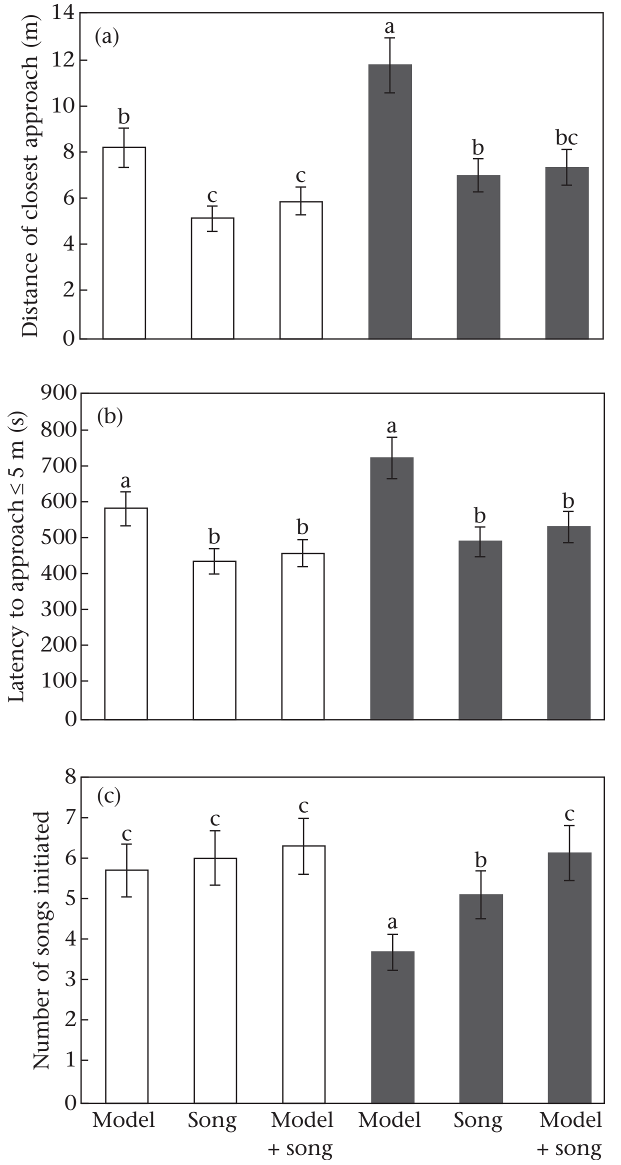

Figure 4. Responses of rufous-and-white wrens (white bars) and banded wrens (black bars) to model presentation (model), song playback (song) and model presentation + song playback (model + song). (a) Distance of closest approach to the playback speaker and/or model. (b) Latency to approach within 5 m of the playback apparatus. (c) Number of songs initiated (number of solos plus first song of a duet). Different letters above bars indicate statistical significance. Graph shows mean + SE values from subject species × treatment type post hoc pairwise comparisons.

obstruction caused by vegetation in the territories of rufous-and-white wrens versus banded wrens at any distance (Table 2). Rufous-and-white wren territories had, on average ± SE, 34.8 ± 3.3% visual obstruction caused by the vegetation when values for all distances were combined, whereas banded wren territories had 30.2 ± 2.6% visual obstruction (Table 2). In other words, between 5 and 15 m, approximately one-third of the area 1 m from the ground was obscured by vegetation in the territories of both species.

We further tested our second prediction that banded wrens would rely more on the visual signal than rufous-and-white wrens by comparing their responses to the treatments with models versus songs. We found a significant difference only in the number of songs initiated by rufous-and-white wrens and banded wrens to the model treatment and the model + song treatment for the number of songs initiated (Table 1). Interestingly, for the response variable 'number of songs initiated', banded wrens sang the fewest songs for the model treatment, the most songs for the model + song treatment, and an intermediate number of songs for the song treatment (Fig. 4c, Supplementary Table S3). Conversely, rufous-and-white wrens did not differ in the number of songs sung in response to the three treatment types (Fig. 4c, Supplementary Table S3).

Rufous-and-white wrens had significantly fewer acacia trees in their territories (just a third the number of acacia trees) compared to banded wren territories. We calculated the number of acacia trees per hectare of territory for both species and, as expected, banded wrens had significantly more trees per hectare (Mann–Whitney *U* test: $U = 1.0$, $P < 0.0001$; Table 2).

Asymmetrical Aggression Response

To test our third prediction that smaller-bodied banded wrens would show equivalent responses to both conspecific and congeneric treatments but larger-bodied rufous-and-white wrens would show stronger responses to conspecific stimuli, we were interested in the interaction between subject species × stimulus species. We found no significant difference in the response to stimulus treatments for either species in their distance to closest approach (Fig. 5a) or latency to approach within 5 m of the loudspeaker (Table 1, Supplementary Table S2). The number of songs initiated was the only response measure that showed a significant effect of the subject species × stimulus species interaction (Table 1). Rufous-and-white wrens sang significantly more songs in response to conspecific versus congeneric trials whereas banded wrens sang a similar number of songs in response to both conspecific and congeneric trials (Fig. 5b, Supplementary Table S3). Rufous-and-white wrens overall sang more duets than banded wrens, but neither species differed in the number of duets they created in response to the conspecific or congeneric trials (Supplementary Table S4). Only the response variable 'number of songs initiated' supported our third prediction.

Responses of Males and Females

To test our fourth prediction that males would respond more strongly than females but that both sexes would respond similarly to the different treatment types, we were interested in the sex × treatment type × stimulus species interaction effect. We found that males approached the playback more closely and had a

Table 2
Results from Mann–Whitney *U* tests comparing vegetation visual obstruction and resource abundance between species' territories

	Rufous-and-white wren	Banded wren	*U*	*P*
% Concealed at 5 m	9.64±2.13	11.36±2.47	204	0.51
% Concealed at 10 m	35.95±4.25	31.14±3.3	204.5	0.52
% Concealed at 15 m	58.75±4.26	48.01±3.99	6	0.07
Number of acacia trees/ha	2.47±0.84	52.61±3.1	**1.0**	**<0.0001**

Significant values shown in bold.

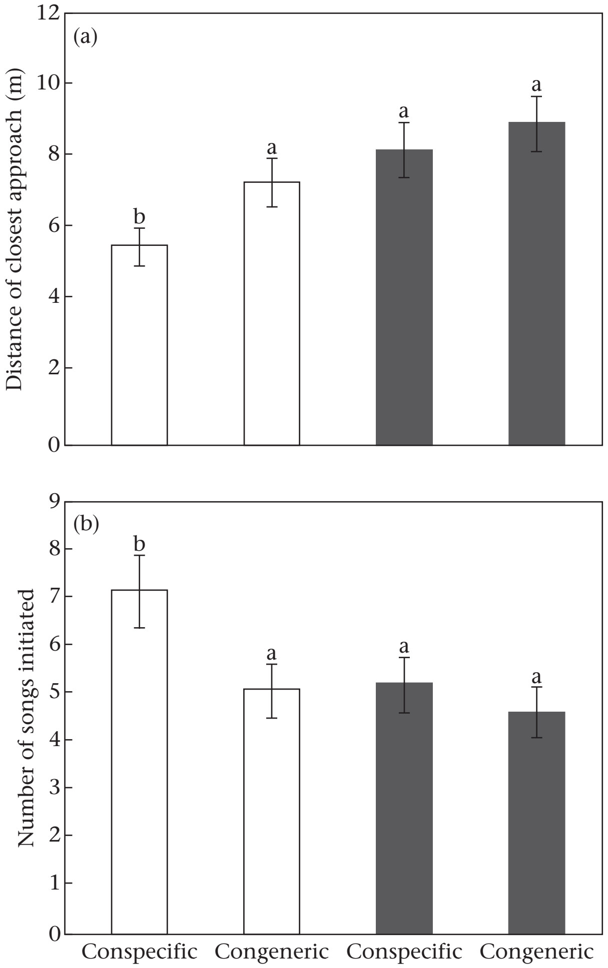

Figure 5. Responses of rufous-and-white wrens (white bars) and banded wrens (black bars) to conspecific and congeneric treatments. (a) Distance of closest approach to the playback speaker and/or model. (b) Number of songs initiated (number of solos plus first song of a duet). Different letters above bars indicate statistical significance. Graph shows mean + SE values from subject species × stimulus species post hoc pairwise comparisons.

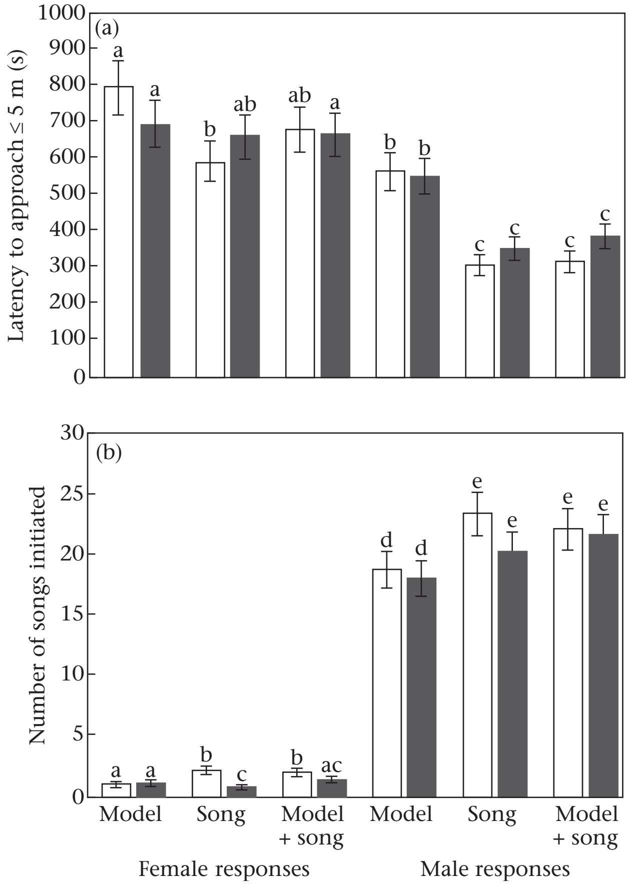

Figure 6. Response of males and females to model presentation (model), song playback (song) and model presentation + song playback (model + song) of conspecific and congeneric stimuli. White bars represent conspecific treatments and grey bars represent congeneric treatments. (a) Latency to approach within 5 m of the playback apparatus. (b) Number of songs initiated (number of solos plus first song of a duet). Different letters above bars indicate statistical significance. Graph shows mean + SE values from sex × treatment type × stimulus species post hoc pairwise comparison.

shorter latency to approach within 5 m of the loudspeaker than females for all treatments (Table 1, Supplementary Table S1). Within the conspecific and congeneric trials, males approached more closely and had a shorter latency to approach within 5 m of the loudspeaker for the model + song treatment and the song treatment than for the model treatment, but there was no difference between the model + song treatment and the song treatment (Fig. 6a, Supplementary Tables S1 and S2). Females did not differ in their distance of closest approach for any of the conspecific or congeneric treatments (Supplementary Table S1), but they did approach within 5 m of the playback apparatus more quickly for the conspecific song treatment than for the model treatment (Fig. 6a, Supplementary Table S2).

Overall, as predicted, males initiated significantly more songs than females (Supplementary Table S3). For both the conspecific and congeneric trials, males sang the fewest songs in response to the model treatment and did not differ in their response to the song treatment and the model + song treatment (Fig. 6b, Supplementary Table S3). For the conspecific treatments, females showed the same response as males: they sang more songs in response to the song treatment and the model + song treatment and the fewest songs in response to the model treatment (Fig. 6b, Supplementary Table S3). For the congeneric treatments, females sang significantly more songs in response to the model + song treatment than in response to the song treatment, but they did not differ in their responses to the model versus model + song treatments or the song versus model treatments (Fig. 6b, Supplementary Table S3). Conversely, females created more duets than males (Supplementary Table S4), but there was no difference in males' responses to any of the conspecific or congeneric treatment types (Supplementary Table S4). Females sang significantly more songs only in response to the model + song treatments versus the model treatment (Supplementary Table S4).

Effect of Playback Order

Playback order was significant for all four response measures (Table 1). However, post hoc comparisons revealed that for distance of closest approach, there was only a significant difference between the trial that was presented first versus fifth ($t_{461} = 3.01$, $P = 0.04$), and for latency to approach within 5 m of the playback apparatus, there was only a significant difference in the trials presented third versus fifth ($t_{461} = 3.12$, $P = 0.03$). There was a significant difference between the first and sixth treatment for the number of songs initiated ($t_{461} = 4.13$, $P = 0.001$), as well as for the number of duets created ($t_{461} = 3.66$, $P = 0.004$), with birds singing fewer songs in response to the last treatment.

DISCUSSION

We investigated the use of acoustic and visual signals for species discrimination in two congeneric Neotropical wren species: rufous-and-white wrens and banded wrens. Both species showed the strongest responses to the song treatment and the model + song treatment, and the weakest response to the model treatment, although there was one instance where the model + song treatment received the strongest response (i.e. the number of songs initiated by banded wrens). Therefore, as predicted, both species rely more on acoustic signals for interspecific discrimination and rely less on visual signals such as plumage coloration. Contrary to our predictions, we did not find significant differences in the vegetation density of the territories of our two study species and only one response variable suggested that banded wrens rely more on the visual signal than rufous-and-white wrens. Interestingly, the two species differed in their responses to conspecific versus congeneric signals. Rufous-and-white wrens showed a stronger response to the conspecific trials than to the congeneric trials, but banded wrens did not differ in their response to conspecific versus congeneric trials. Our results show that birds living in densely vegetated habitats use vocal and visual traits as intra- and interspecific discrimination signals, but that they rely more on acoustic communication.

Rufous-and-white wrens are monochromatic, with birds of both sex exhibiting similar plumage coloration. However, the sexes have obvious dimorphic song features, where females sing quieter songs with shorter trill components and higher-frequency elements (Mennill & Vehrencamp, 2005). Males and females also sing separate repertoires of songs, which may facilitate individual identification within their own species (Mennill & Vehrencamp, 2005). These pronounced sex and individual differences in vocalizations may explain why rufous-and-white wrens rely more on acoustic signals for intraspecific discrimination. Furthermore, the songs of rufous-and-white wrens and banded wrens differ substantially in their length and frequency (Fig. 2) and, consequently, sound very distinct. Their plumage, however, is relatively similar, with rufous brown coloration above and white below, with the primary difference being the dark barring on the flanks of banded wrens (Fig. 2). Additionally, the plumage of both species is relatively drab and does not stand out against the brownish bark and leaf litter of the tropical dry forest (see Doucet, Mennill, & Hill, 2007). Given the similarity in their plumage, and the dissimilarity in their voice, it is not surprising that these species should rely heavily on acoustic signals and less on visual signals for interspecific discrimination.

Only three previous studies have investigated the simultaneous use of both visual and acoustic signals for species discrimination in birds. One ground-breaking study compared the response of two sister taxa from the *M. castaneiventris* complex of the Solomon Islands: the chestnut-bellied form, *M. castaneiventris castaneiventris*, and the white-capped form, *M. castaneiventris richardsii* (Uy et al., 2009). When these two species were presented with matching or mismatching taxidermic mounts and songs, they both used song and plumage for discrimination, but they relied more heavily on plumage (Uy et al., 2009), in direct contrast to our findings. Another study on *Monarcha* flycatchers found that subspecies in more densely vegetated forests use acoustic and visual signals sequentially, using song for long-range recognition and plumage for close-range discrimination (Uy & Safran, 2013); by contrast, subspecies in more open habitats use song and plumage simultaneously (Uy & Safran, 2013). These two studies show that birds are able to use both acoustic and visual signals for species discrimination but that they may differ in their use of these signals depending on their habitat. Further research is needed to demonstrate whether rufous-and-white wrens and banded wrens use song and plumage sequentially in their tropical forest habitat. Future studies comparing signal use in habitats with differing vegetation density are required to demonstrate the influence of vegetation density on multimodal signalling in birds. The vegetation density at our study site was moderately high, so we would expect birds to rely more on the visual signal in a less densely vegetated habitat or if they have plumage that contrasts against the background. We found that banded wrens initiated the most songs in response to the model + song treatment, the least number of songs for the model treatment, and an intermediate number of songs for the song treatment. These findings suggest that although banded wrens rely on acoustic signals, the addition of the visual signal strengthens their response.

Rufous-and-white wrens were more responsive and they responded more strongly to conspecific than to congeneric stimuli, whereas banded wrens responded with similar intensity to both conspecific and congeneric stimuli. Such interspecific variation in responses could be indicative of interspecific dominance between these two species. Rufous-and-white wrens showed a lower response to the banded wren stimuli and did not differ in their response to the different congeneric treatments, suggesting that rufous-and-white wrens may not perceive banded wrens as a strong threat. Conversely, banded wrens responded to conspecific and congeneric stimuli as though they were equally threatening. One possible explanation is that banded wrens failed to differentiate between conspecific and congeneric stimuli (Murray, 1981). However, the substantial difference in the length, frequency and amplitude of the songs of these two species (Fig. 2c) makes this explanation seem unlikely, especially with the additional presentation of visual signals for many of the treatments. The presence of interspecific dominance seems a more plausible explanation. Other species showing interspecific dominance also demonstrate asymmetry in their responses to congeneric versus conspecific signals (Martin & Dobbs, 2015; Martin & Martin, 2001; Pearson & Rohwer, 2000). In chickadees, for example, dominant black-capped chickadees were more vocal and responded more strongly to conspecific than heterospecific calls, whereas subordinate mountain chickadees responded similarly to both mountain and black-capped chickadee calls (Grava et al., 2012). Other indirect evidence supports the dominance of rufous-and-white wrens over banded wrens. For example, rufous-and-white wrens have larger territories (1.35 ± 0.10 ha, Mennill & Vehrencamp, 2008) than banded wrens (0.40 ha, Trillo & Vehrencamp, 2005). In addition, rufous-and-white wrens are larger (body length: 14.5–16.5 cm; Brewer, 2001) and heavier (males: 25.8 g; females: 23.7 g; Mennill & Vehrencamp, 2005) than banded wrens (14–15 cm; Brewer, 2001; males: 20.3 g; females: 18.3 g; Hall et al., 2015); larger body size has previously been shown to relate to interspecific dominance (Farwell & Marzluff, 2013; Freshwater, Ghalambor, & Martin, 2014; Funghi, Leitão, Ferreira, Mota, & Cardoso, 2014). To conclude that these two species are ecological competitors, further research is required to assess whether banded wrens suffer fitness costs when living in sympatry with rufous-and-white wrens, and whether rufous-and-white wrens restrict the distribution of banded wrens. Another possible explanation for our findings is that banded wrens may have higher-quality territories, in terms of the number of nesting acacia trees, and they must defend their territories against not only conspecific but also congeneric competitors. Rufous-and-white wrens, on the other hand, may have lower-quality territories, in terms of the number of nesting acacia trees, and may be less likely to be usurped by congeneric competitors. It would be necessary to assess other aspects of territory quality (e.g. food availability, etc.) before concluding that banded wrens have better-quality territories than rufous-and-white wrens.

Consistent with previous studies, we found that males were significantly more responsive to playback than females in both species (Fedy & Stutchbury, 2005; Hall et al., 2006; Mennill, 2006; Mennill & Vehrencamp, 2008). In our study, however, the two sexes differed in their response to the different treatment groups. For all of our response variables except number of duets created, males appeared to show the lowest response to the model treatment and a stronger, equivalent response to the model + song treatment and the song treatment for both the conspecific and congeneric trials. Females, by contrast, only showed this response for the number of songs initiated in response to the conspecific trials, and for many of the other measures, they did not differ at all in their response to the three treatment types. These results could be due to the lower response rate of females, which may not have allowed us to statistically differentiate between the three treatments.

Rufous-and-white wrens and banded wrens live in a tropical dry forest characterized by dense vegetation. Our analyses suggest that, on average, vegetation obstructs 35% of the visual signals in rufous-and-white wren territories and 30% in banded wren territories (Table 2), even at distances as close as 10 m, demonstrating that visual signals have limited transmission capabilities. Contrary to our predictions, the understory vegetation density in the habitats of each of our two focal species was not significantly different. These findings could have been affected by the fact that the measurements were taken during the beginning of the rainy season, when the tropical dry forest habitat of banded wrens starts to become more similar to the evergreen habitat of rufous-and-white wrens. Our vegetation measurements also revealed that banded wren territories contained significantly more acacia nesting trees than rufous-and-white wren territories. Rufous-and-white wrens may need to defend nesting trees more aggressively because acacia trees are limited in their more mature evergreen habitat compared to the less mature dry-forest habitat of the banded wrens.

One potential limitation of our study is that it relied on the use of wooden models to serve as a visual representation of conspecific and congeneric animals. This is the first study to use both avian wooden models and song playback to investigate the importance of visual and acoustic signals for inter- and intraspecific discrimination. Our successful use of avian wooden models provides an alternative to sacrificing study animals to create taxidermic mounts. Although our wooden models were realistic (see Figs. 1 and 2), and the colour approximated the plumage reflectance of museum specimens, the lack of movement may have hindered the response of the birds. If the models produced movements such as wing flaps or tail cocking, they may have elicited stronger aggressive responses (Anderson et al., 2013). Experiments involving robotic birds (e.g. Balsby & Dabelsteen, 2002; Patricelli, Coleman, & Borgia, 2006) show that movements can influence responses to model presentation experiments. Moreover, a previous study showed that birds use not only colour but also surface texture as a signal for species discrimination (Němec et al., 2014). Red-backed shrikes, *Lanius collurio*, attacked a taxidermic model of a predator Eurasian jay, *Garrulus glandarius*, more often than a plush model, and attacked a silicone model the least (Němec et al., 2014). Although our wooden models had feather-like texture carvings and looked more realistic than the plush model used in the aforementioned study (see Figs. 1 and 2), the use of a taxidermic mount with feathers that rustled in the wind might have elicited a stronger response. Nevertheless, banded wren males sang the most songs to the model + song treatment, and in one instance, a rufous-and-white wren attacked the model, which suggests that the birds were responding to the visual model.

Our study demonstrates that wrens living in tropical forests rely primarily on acoustic signals for inter- and intraspecific discrimination. We expect similar patterns among other species that have distinct songs but similar or cryptic plumage, especially in dense habitats with visual obstruction. The asymmetry in response to congeneric versus conspecific stimuli suggests the possibility of an interspecific dominance relationship between rufous-and-white wrens and banded wrens, which could have significant implications if shared resources become scarce and rufous-and-white wrens outcompete subordinate banded wrens. This is the first study to investigate multimodal signal use in both males and females in tropical habitats, and our experiment revealed that the use of different signal modalities and the strength of responses can vary both within and among species. More studies are needed to determine the breadth of these patterns and how they vary across habitats and across species that differ in visual or acoustic conspicuousness.

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Supplementary Material

Supplementary material associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.anbehav.2016.05.024.

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